



Ants (Hymenoptera: Formicidae) and ecosystem functions and services in urban areas: a reflection on a diverse literature

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Abstract

Urban environments are the fastest growing ecosystems on Earth. Ants are among the most abundant arthropod taxa in urban ecosystems and provide important ecosystem services. Here, we review the literature on ecosystem services provided by ants in urban ecosystems and examine how these services are affected by urbanization. In particular, we examine the role of ants in seed dispersal, soil enhancement, scavenging of urban food waste, and pest control. We also examine how urbanization affects trophic interactions involving ants, including mutualistic interactions with hemipterans, and how this affects the ecosystem service of pest control in cities. We found that the potential for ants to provide ecosystem services in urban areas depends on how the ant community is affected by urbanization and the resulting species composition. In some cases, the remaining species are highly effective, but in other cases, the most efficient species decline or are replaced by less efficient species as urbanization proceeds. Because these services depend on the structure of ant communities, which, in turn, is predicted to be altered by climate change, we also examine the effect of climate change on ant communities in the urban environment, including interactions between urbanization and climate change. The ants that persist in urban environments are largely those with broader temperature ranges and higher heat tolerance, whether by increasing the minimum or maximum temperature that the ants can tolerate.

Key words: Ant-mediated ecosystem services, cities, climate change, invasive species, myrmecochory, pest control, review, scavenging, soil enhancement.

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Introduction

Urban landscapes cover only 3% of the Earth's surface but hold 54% of the human population. These landscapes are influenced by the social, cultural, and economic conditions of the communities living in them. The process of urbanization is frequently cited as one of the leading causes of habitat loss producing high rates of local species extinctions, frequently eliminating most of the native species (CZECH & al. 2000, MARZLUFF 2001, MCKINNEY 2006, 2008). Many native species are then replaced by “weedy” non-native species, constituting a process of biotic homogenization, which becomes more evident at the core of urban areas (BLAIR & LAUNER 1997, MCKINNEY 2006, KOWARIK 2008).

Despite the fact that city landscapes are more similar to one another than they are to the surrounding rural landscapes, green spaces within urban areas are highly heterogeneous. The many distinct and small habitat patches

within the urban matrix can give rise to a surprising number of species and provide many unexplored opportunities for biodiversity conservation (LEPCZYK & al. 2017). The potential of these landscapes to support biodiversity and also to connect citizens with nature is increasingly being recognized (PRÉVOT & al. 2018).

Beta diversity is highly variable, and trends in changes of species richness between different urban habitats differ between plants, mammals, avian species, and groups of invertebrates (FAETH & al. 2011, DALLIMER & al. 2012, PHILPOTT & al. 2014, NAGY & al. 2018). As urban development continues to overtake the surrounding landscapes, it is essential for biodiversity conservation that we understand how this transformation affects the abundance and distribution of species.

Ants are a dominant taxon of most terrestrial ecosystems and a ubiquitous component of the arthropod fauna

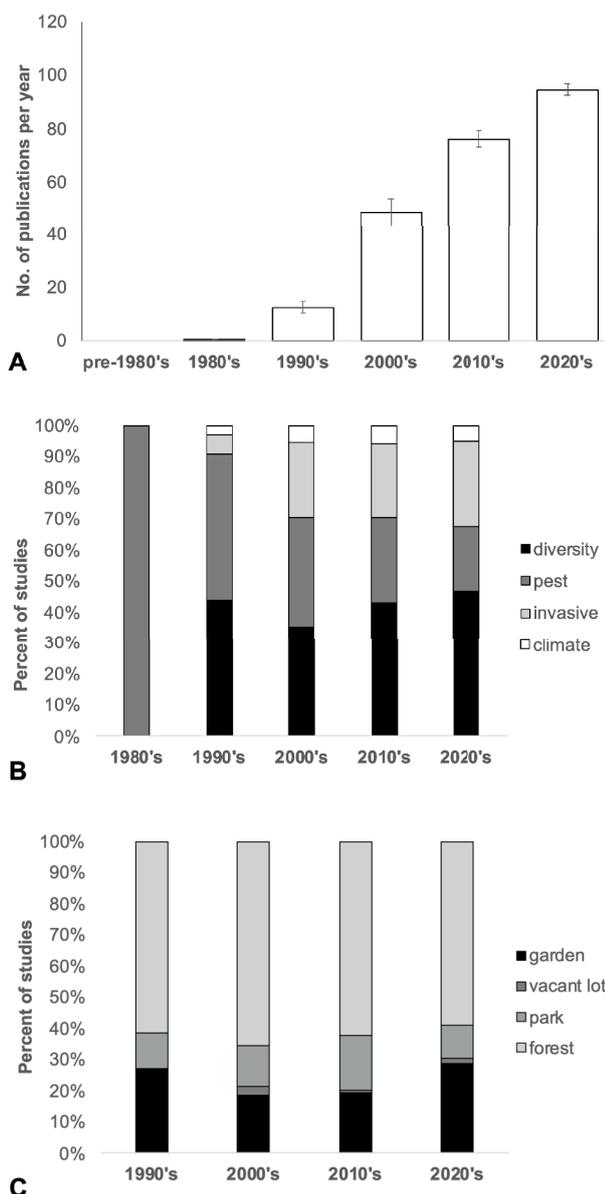


Fig. 1: Summary of information from a Web of Science search for “ants” or “Formicidae” and “urban”, with a focus on the increase in number of studies on urban ants since the 1990’s of the 1595 studies recorded (A), a shift in the percent of papers covering the four listed topics over time (B), and a relatively constant focus on multiple urban habitats between 1990 and 2022 (C).

of almost all cities, playing important roles (both positive and negative) in the ecology of cities (SANFORD & al. 2009, MADDEN 2010, SANTOS 2016). They are an ideal taxon for exploring general aspects of urban biodiversity as their size and species diversity can be captured in very small areas, and they are among the most abundant arthropod taxa in cities (YOUNGSTEADT & al. 2015, SANTOS 2016). This has led to a substantial number of independent studies (see, for example, GUÉNARD & al. 2015, OSSOLA & al. 2015, VONSHAK & GORDON 2015, SANTOS 2016, MIGUELENA & BAKER 2019, PEREZ & DIAMOND 2019, SANTOS & al.



Fig. 2: Urban habitats that have been studied by myrmecologists. A) Stacy Philpott and her student, Russ Friedrich, sampling ants in an urban park and an urban forest (in the background) in Toledo, OH (UNO & al. 2010); B) Denisha Parker, a student of Mary Gardiner, sampling insects in a vacant lot in Cleveland, OH (GARDINER & al. 2013, 2014); C) Stacy Philpott and her students Bella Mayorga, Azucena Lucatero, and Monika Egerer, sampling ants and other insects in an urban garden in San José, CA (PHILPOTT & al. 2020); D) Amy Savage studying ants in a Broadway street median in New York City, NY (PENICK & al. 2015).

2019), suggesting an overview is in order. Previous reviews (CAMPOS-FARINHA 2005, SANTOS 2016) note that very few published studies on ants are from urban environments (only 3.6%, according to SANTOS 2016) and almost all are related to their role as pests in the human-built environment, especially within houses, hospitals, and other buildings. These studies discuss the potential disservices caused by ants in urban environments, including damage to infrastructures and buildings, contamination of stored food, direct harms to humans through painful stings (for example, the electric ant *Wasmannia auropunctata*, and the red imported fire ant, *Solenopsis invicta*), and serving as vectors of pathogens (KLOTZ & al. 2003, OLAYA-MAS-MELA & al. 2005, SILVERMAN 2005, DEL TORO & al. 2012, DE CASTRO & al. 2016). The objective of this review is to summarize and synthesize the literature on the subject of ants in the urban landscape with a focus on how ants contribute to the functioning of urban ecosystems and identify knowledge gaps that can guide future research on urban ants and ecosystem services.

Burgeoning interest in urban ecology in recent years has resulted in many studies examining ant assemblages in urban areas outside buildings, in a variety of habitats (Figs. 1 & 2). A Web of Science search in June 2022 for studies that included “ants” or “Formicidae” and “urban” yielded 1595 studies, with a steady increase in papers per year since the 1990’s (Fig. 1A). Moreover, over the past two decades, the topics of published studies has moved away from a focus on ants as urban pests to an inclusion of themes like diversity, invasive species, and climate change (Fig. 1B). These studies have examined ants in multiple habitat types such as parks, urban forests, gardens, yards,

and street medians (Figs. 1C, 2). In particular, interest has shifted from the vision of ants as pests in homes and hospitals (BERTONE & al. 2016, DE CASTRO & al. 2016) to the positive aspects of ants in the urban environment. Many ant species can render “ecosystem functions” and even “services”, which is to say, ants are providers of benefits to humans. Since climate change has been shown to affect urban environments by, for example, an increased heat island effect and flooding (WILBY 2007), it is important to also examine how climate change affects ants living in cities and how these changes may impact the ecosystem services that ants provide. An increasing number of studies are documenting how climate change impacts the urban environment and the diversity of organisms therein, including ants (ANGILLETTA & al. 2007, LIN & al. 2015, OSSALA & al. 2015, CROSS & al. 2016, DIAMOND & al. 2017, PEREZ & DIAMOND 2019). This review thus focuses on ants as ecosystem service providers (and in some cases disservices), with the added element of how expected impacts of climate change may be an integral force thereof.

Ecosystem functions and services: the ant connection

Ecosystem functions are natural processes that take place in all ecosystems, whereas ecosystem services are ecosystem functions that are directly beneficial to humans (DAILY 2003, MILLENNIUM ECOSYSTEM ASSESSMENT 2005). Ants are involved in both ecosystem functions and services (DEL TORO & al. 2012, 2015). Ant diversity and composition changes with the degree of urbanization, and such changes can have important implications for the ecosystem functions and services that ants provide in the urban environment (SANFORD & al. 2009). Few studies have examined the ecosystem functions and services provided by ants in urban landscapes; these can be grouped into seed dispersal, soil enhancement, scavenging, and pest control (Fig. 3, Tab. 1).

Seed dispersal

Myrmecochory (seed dispersal by ants; Fig. 3A) is a geographically widespread phenomenon involving at least 11,000 plant species (LENGYEL & al. 2010). It has been estimated that in some temperate woodlands ants disperse up to 40% of the herbaceous plants, making myrmecochory an important ecological process for the maintenance of plant diversity in these ecosystems (BEATTIE 1985). In one of the first studies of ecosystem services by ants in urban landscapes, THOMPSON & MCLACHLAN (2007) documented the role of ants in seed dispersal of the myrmecochorous plant, *Viola pubescens*, in urban forests in Manitoba, Canada. The removal rate of seeds of *V. pubescens* was higher in urban forests than in rural forests, even though ant species richness in urban forests was lower. The authors attributed the increased removal rate in urban forests to changes in the species composition of the ant community. The ant species that remained in urban forests tended to be the most competitively dominant species, which apparently were also more efficient seed dispersers. Members



Fig. 3: Depictions of four major ecosystem services provided by ants in urban areas: A) seed dispersal (*Aphaenogaster fulva* dispersing bloodroot (*Sanguinaria canadensis*) seeds; photo by Alex Wild); B) soil ecosystem services (sidewalk in Ann Arbor, MI, with nests of *Tetramorium immigrans*); C) scavenging of human food waste (*Solenopsis geminata* scavenging on tortilla chips in a sidewalk in Tapachula, Mexico); D) biological pest control (*Aphaenogaster rudis* preying on an unidentified larva in an urban garden in Ann Arbor, MI).

of the *Formica fusca* group, for example, are among the most effective forest-dwelling foragers, persist in urban forests, exhibit competitive release when interference at food resources from superior competitors is removed (SAVOLAINEN & VEPSÄLÄINEN 1988), and are well-known seed dispersers (PUDLO & al. 1980). A recent review of global rates of seed dispersal and seed predation in different environments found that human dominated habitats (like urban and agricultural areas) have a higher prevalence of seed dispersal than most other habitats (except forests) but also exhibited high variability (PENN & CRIST 2018).

Urban forests tend to be isolated patches with a reduced area, sharp edges, and a high proportion of edge habitat (HAMBERG & al. 2009). Studies of ants in forest edges as compared with non-edge habitats have yielded variable results, with some studies reporting increases, others reporting reductions, and yet others reporting no change in ant species richness and abundance (for reviews, see CRIST 2009). However, relatively few of these studies have been conducted in urban forests as compared with natural forests or agricultural sites (CRIST 2009). The most consistent results for urban forest studies have been changes in species composition in forest edges, with higher proportion of aggressive dominant species and invasive species in edges as compared with forest interiors (SUAREZ & al. 1998, BOLGER & al. 2000, HOLWAY 2005, LESSARD & BUDDLE 2005, CRIST 2009, IVANOV & KEIPER 2010).

Non-native and invasive species can disrupt myrmecochory by displacing the ant species involved in tight myrmecochory interactions (ZETTLER & al. 2001, CARNEY & al. 2003). In one case, in an urban park outside of Melbourne, Australia, seed removal and seed dispersal distance were much more variable for both native (e.g., *Acacia retinoide*) and non-native (e.g., *Polygala myrtifolia*) seeds as a result

of replacement of native seed dispersing ants by *Linepithema humile* (see ROWLES & O'DOWD 2009). Additionally, bloodroot (*Sanguinaria canadensis*) has shorter seed dispersal distances in forest fragments invaded by the red imported fire ant, *Solenopsis invicta*, because they were less effective at dispersing seeds (NESS 2004). Since these ants penetrate into the forests from the edges, we would expect myrmecochory to be more disrupted in forest edges as compared with the interior.

A study of exurban development (second homes in woodland sites) found a change in the behavior of *Aphaenogaster rudi*, an important seed disperser. In forest edges, *A. rudi* generally moved the seeds away from the edges and toward the woodland interior, which correlated with an increased density of myrmecochorous herbs in forest interiors as compared with edges (WARREN & al. 2015). Similar observations have been made for the same and other *Aphaenogaster* species in North America (NESS 2004). In fact, NESS & MORIN (2008) argue that the paucity of ants engaged in myrmecochory contribute to the rarity of ant-dispersed plants in forest edges relative to interiors. Thus, although the role of myrmecochory in urban forests can be particularly critical for spring flora in temperate forests (BEATTIE & al. 1979), this could be threatened by changes in ant species composition and, in particular, species behaving like invasive species. Since urban forests tend to be smaller and have a higher perimeter to interior ratio than forests in rural environment (MEDLEY & al. 1995), we would expect these negative forest edge effects on myrmecochory (i.e., higher proportion of dominant or invasive species and dispersal from edge toward forest interior) to be stronger in urban forests. Forest edge effects could also result in a lower density and diversity of herbaceous myrmecochorous plant species in forests within cities as compared with forests in rural areas. Future studies of myrmecochory in urban environments could test this hypothesis and also test the hypothesis that there should be a positive association between diversity and abundance of myrmecochorous plant species and the size of urban forests.

It should also be noted that recent herbaceous-plant-removal experiments and short-term seed supplementation experiments suggest that myrmecochory does not always result in benefits for the ant partner. In some cases, myrmecochory even has negative effects (ant colony health in the long term was found to be higher in areas where elaiosome-bearing plants were removed) (WARREN & al. 2019). These results call into question the assumption of myrmecochory as a constant mutualism.

Soil enhancement

The role of ants in soil processes has received considerable attention (see reviews by DE BRUYN & CONACHER 1990, FOLGARAIT 1998, VANDERMEER & PERFECTO 2007, CAMMERAAT & RISCH 2008, SWANSON & al. 2019). Ants enhance soil structure and aggregate stability, lower bulk density, and increase aeration and water infiltration due to their burrowing activities (CAMMERAAT & RISCH 2008,

FROUZ & JILKOVA 2008). Generally, within or close to their nests, there is a high concentration of soil nutrients and increased nitrogen and organic matter cycling (CAMMERAAT & RISCH 2008, FROUZ & JILKOVA 2008). However, very little is known about how these ant-mediated soil ecosystem functions are affected by urbanization or how these soil-related ecosystem services by ants are manifested in urban environments. The few studies that have examined soil ecosystem services of ants in urban or urbanizing environments show both negative and positive effects of urbanization on ant-mediated soil enhancement.

SANFORD and colleagues (2009) documented the changes in ant communities that have important soil-related ecosystem functions in forest landscapes as land development and urbanization increase. They classified the ants into three groups: 1) aerator ants that build complex subterranean tunnels that aerate the soil and help with water infiltration as well as energy redistribution; 2) decomposer ants that build tunnels within woody debris facilitating decomposition; and 3) compiler (thatch) ants that build mounds with vegetation increasing soil nutrient availability through higher mineralization rates of nitrogen and organic matter. This study, conducted in the Lake Tahoe basin, concluded that high levels of land development significantly reduce the diversity and abundance of aerators and decomposers, potentially reducing the soil-mediated ecosystem functions of these species in urbanized landscapes (SANFORD & al. 2009). However, significant drops in species richness of these two groups were detected only above 30-40% of land development, suggesting that the ant community can be robust to limited amounts of land development. This study also found that thatch ants, which are associated with higher localized soil nutrient availability, were positively associated with urban development, although their overall abundance was low compared with all the other groups of ants (SANFORD & al. 2009).

It is possible that urbanization, rather than changing the abundance of particular species, changes other species characteristics that influence soil ecosystem services. For example, in a study in Brazil, it was found that although nests of leaf cutter ants were similar in urban and rural environments, the urban nests had more chambers than the rural nests (SANTOS LOPES & al. 2011). This may suggest a stronger role of these ants in soil turnover in urban areas.

Although there are many studies that have documented the role of ants in soil-related ecosystem functions and services (DE BRUYN & CONACHER 1990, FOLGARAIT 1998, VANDERMEER & PERFECTO 2007, CAMMERAAT & RISCH 2008, SWANSON & al. 2019), we were able to find only two studies examining how urbanization may affect ant-mediated soil ecosystem services. Furthermore, neither of these studies measured the ecosystem service or ecosystem function directly. Rather, they documented changes in ant species that have been implicated in soil ecosystem services. Future research on this topic should establish a direct connection between urbanization and ant-mediated soil ecosystem services. Another possible avenue of

research related to the impact of ants on soils in urban environments is the effect of the pavement ant, *Tetramorium immigrans* (formerly *Tetramorium caespitum* (LINNAEUS, 1758) FLUCHER & al. 2021), on soil aeration and water infiltration. NUHN & WRIGHT (1979), conducting surveys of ants in suburban habitats in Raleigh, North Carolina, observed that soil beneath sidewalks was a common location for nests of certain ant species, in particular, the pavement ant, which nests under bricks and concrete and in sidewalk crevices (Fig. 3B). To our knowledge, no study has been conducted to date quantifying the effect of this species on soil aeration and increases in water infiltration rates in urban areas. Based on the high density of this species along pavements in cities (PEĆAREVIĆ & al. 2010), this effect could be important.

Scavenging

Generalist ants, which increase in abundance in urban environments (SANTOS 2016), tend to be scavengers. Urban ants are important in removing food waste in highly urbanized environments (PENICK & al. 2015, YOUNGSTEADT & al. 2015, HOSAKA & al. 2019). The removal of food waste by ants can be an important ecosystem service because it reduces the amount of food available to rats and other arthropods that can be vectors of human diseases (Fig. 3C). In a study in Manhattan, New York City, PENICK & colleagues (2015) found that arthropods, primarily ants, removed between 32 and 59% of experimentally placed food (pieces of potato chips, cookies, and hotdogs) within 24 hours and that the removal rate depended on food size. Surprisingly, food removal from street medians was 2 to 3 times higher than the removal rates in parks, even though medians had a lower species diversity. The difference was attributed to the presence of the pavement ant, *Tetramorium* sp. E (most likely *T. immigrans*, formerly known as *Tetramorium caespitum*, see STEINER & al. 2008), which occurs in high abundance in highly urbanized environments. Assuming five to eight months of ant activity and an average of nine *T. sp. E* foraging territories on a single 400 m² median, the authors estimated that on the order of 4 to 6 kg of food waste per median per year is removed by arthropods, primarily ants, in Manhattan. Using isotope analysis, another study showed that urban *T. sp. E* individuals had a stable isotope signature associated with human processed food and that the signal increased with the level of urbanization (PENICK & al. 2015). The high scavenging rate in Manhattan street medians appears to be due almost exclusively to the presence of the pavement ant. Cities without this species may show a very different pattern of scavenging by ants. For example, in a study conducted along a gradient from forest to city in Singapore, the pattern of dead insect removal was found to be the opposite, with a high removal rate in forested sites as compared with urban parks and pavements (TAN & CORLETT 2012). In this study, the highly urbanized sites recorded the lowest rate of dead insect removal by ants, although these areas had non-native tramp ants such as *Anoplolepis gracilipes*, *Monomorium pharaonis*,

Paratrachina longicornis, *Pheidole megacephala*, and *Tapinoma melanocephalum*. Although this study was conducted with non-human waste food, it suggests that not all scavenger ants, including non-native species, have a high removal rate within cities. The main difference between these studies seems to be that the pavement ant was absent from the sites in Singapore. In a more recent study in Tokyo, HOSAKA & colleagues (2019) demonstrated that ants sampled in urban and suburban areas removed between 6.8 and 18.0 g of experimentally placed food (e.g., potato chips, cookies, and ham) from woodland, lawn, and pavement. They found that the occurrence frequency of commonly encountered ant species differed with the urban habitat type, as did species richness, and food removal was higher on lawns compared with pavement. Although food removal rates were not associated with changes in ant species richness, food removal rate on lawns was positively associated with occurrences of *Tetramorium tsushimae*, and removal on pavement was negatively associated with occurrences of *Monomorium intrudens*. In a different type of scavenging study, ASHIGAR & AB MAJID (2020) examined the abundance, diversity, and foraging patterns of ants removing cockroaches from latrines in rural and urban areas of Nigeria. They found a higher diversity but similar abundance of ants in urban areas and that the composition of ants removing cockroaches differed in rural versus urban areas. Moreover, they found that *Pheidole* spp. had higher scavenging success rates in urban areas and more effectively removed cockroaches compared with other ant species (e.g., *Camponotus maculatus*, *Brachyponera sennaarensis*).

These studies demonstrate that scavenger ants can provide important scavenging services in cities by removing significant amounts of human food waste (PENICK & al. 2015, YOUNGSTEADT & al. 2015) and that the provisioning of scavenging services is strongly influenced by the composition of species in the various urban habitats, with *Tetramorium* species being responsible for high removal rate of food waste in cities (PENICK & al. 2015, YOUNGSTEADT & al. 2015, HOSAKA & al. 2019). Moreover, ants may provide important scavenging services, such as cockroach removal, potentially providing a public health service within urban households (ASHIGAR & AB MAJID 2020).

Another important aspect to note is that species in disturbed habitats, as most habitat patches in cities, tend to be competitive dominants that have large colonies, and many of them are non-native species. Therefore, the relationship between urbanization (as a disturbance) and scavenging ecosystem services may not be straightforward because species in disturbed habitats may be more effective at removing human food waste compared with the species that are lost by the urbanization disturbance. Removal rates in Tokyo were higher than removal rates in New York City, but in both cases most of the removal was done by species typical of highly disturbed habitats (*Tetramorium* sp. E (most likely *Tetramorium immigrans*) and *Tetramorium tsushimae*). The higher removal in Tokyo as compared with New York City could be due to differences in ant

abundance and activity between the two cities. It has been suggested that removal rates may even be higher in the tropics (HOLLDÖBLER & WILSON 1990). But removal of human food waste has not been quantified in any tropical country. More studies from a broader geographic region could shed light on the role of climate, especially temperature, on ant-mediated scavenging ecosystem services.

Finally, in order to understand removal rates of human food waste by ants, it is important to quantify the other food resources available to ants. For example, PENICK and colleagues (2015) suggested that ants in parks are less likely to forage on human food waste due to higher availability of honeydew from hemipterans on the roots of grasses. Then again, the unusual abundance of human waste resources in some city habitats, like street medians, can influence the population dynamics of some species and may even alter ant community structure by favoring generalist scavenging ants. Human food waste resources can vary with season and may play an important role during periods when other food resources (like natural prey) may be scarce.

Pest control

One of the best documented ecosystem services provided by ants to humans is the service of pest control (WAY & KHOO 1992, PERFECTO & CASTIÑEIRAS 1998, PHILPOTT & ARMBRECHT 2006, OFFENBERG 2015). This can be an important regulatory ecosystem service because it enables sustainable crop production without the reliance on toxic pesticides. Natural pest control by ants has been well documented in agricultural systems especially in the tropics (WAY & KHOO 1992, PERFECTO & CASTIÑEIRAS 1998, PHILPOTT & ARMBRECHT 2006), but few studies have examined this ecosystem service in the context of urban landscapes, where it can be particularly important in urban and peri-urban agriculture, where high population densities can be in close proximity to crop production sites. However, ants can also contribute to pest control not related to agriculture. Here, we examine both agricultural and non-agricultural ant-mediated pest control.

With an increasing proportion of the world's population living in urban areas, urban agriculture has become increasingly important for food security. The Food and Agriculture Organization (FAO) estimates that 15 to 20% of the global food supply comes from urban and peri-urban agriculture (VAN VEENHUIZEN & DANSO 2007, although this figure has been questioned, see CLINTON & al. 2018) with close to 200 million people engaged in this food production activity (ZEZZA & TASCIOTTI 2010). One of the most impressive examples of how urban agriculture can contribute to food security is Cuba, where between 60 and 90% of the total vegetable production is produced in urban and peri-urban agricultural farms (BOURQUE & CAÑIZARES 2001, COMPANIONI & al. 2002). Ant communities and the role of ants as natural biological control agents in Cuban urban and peri-urban farms have been well studied (ALFONSO-SIMONETTI & al. 2010, MATIENZO BRITO & al. 2010). In particular, it is worth mentioning the establishment of

reservoirs for the big-headed ant, *Pheidole megacephala*, which has a long history in Cuba for the control of the sweet potato weevil (*Cylas formicarius*) and the banana weevil (*Cosmopolitas sordidus*) (VÁZQUES & FERNÁNDEZ 2007, PEREZ-CONSUEGRA & al. 2018, MÁRQUEZ & al. 2019). Other examples of ants as biocontrol service providers in urban agriculture include a recent study in urban gardens in California that showed that > 60% of sentinel pests (corn ear worm eggs, *Helicoverpa zea*) were removed from experimental plants in 24h and that removal rates were higher in smaller gardens and in gardens with more woody vegetation (PHILPOTT & BICHER 2017). Although they did not specifically study which predator removed eggs, Argentine ants (*Linepithema humile*) were the most common predators observed on and near to eggs and were likely responsible for most removals of this pest species. Even though Argentine ants may have detrimental effects on the native ant communities where introduced (e.g., SUAREZ & al. 1998), they may nonetheless provide important biocontrol services. In another experiment with sentinel prey in urban gardens in Michigan, EDWARDS (2016) documented *Formica obscuripes*, *Formica subsericea*, and *Tetramorium immigrans* removing cabbage looper (*Trichoplusia ni*) larvae and damaging egg clusters of this important pest of cruciferous crops (Fig. 3D).

Pest control not related to agriculture within cities include the control of noxious insects, like flies and cockroaches, the control of pests in apiculture, and the control of pests of trees. In the 1930s, PHILLIPS (1934) credited *Pheidole megacephala* with keeping the house fly population to negligible levels in Hawaii. However, the first documented case of biological control by ants in an urban setting was PIMENTEL's study of ants controlling fly populations in San Juan, Puerto Rico. After casual observations of the native fire ant, *Solenopsis geminata*, killing fly larvae near garbage bins, PIMENTEL (1955) conducted an experiment with all life stages of *Musca domestica* and found that ants were responsible for killing an average of 91% of the potential fly population between the egg and adult stages. Besides *S. geminata*, other species were observed retrieving larvae but in very low numbers. The only species capable of killing the pupal stage was the small *Solenopsis corticalis*, which was observed boring a hole in the wall of the puparia, entering and consuming the pupae inside. PIMENTEL (1955) attributed the low fly incidence in cities and towns in Puerto Rico to the high abundance of *S. geminata*.

More recent studies of the biocontrol services provided by ants in urban landscapes focus on differences among a variety of urban habitats such as urban parks or forests, vacant lots, and urban gardens. In a study comparing predation of the greater wax moth (*Galleria mellonella*), a parasite of honeybee hives, in two post-industrial cities in Ohio, ants were reported to be responsible for 60% and 33% greater wax moth mortality after 48h of exposure in vacant lots and urban gardens, respectively (YADAV & al. 2012). Due to frequent irrigation, soils in urban gardens were consistently more moist and cooler than in the vacant

lots, and this may have contributed to lower predation activity by ants in gardens as compared with vacant lots (KASPARI & al. 2000, YADAV & al. 2012, but see GARDINER & al. 2014).

Although we could not find any study of ants as biological control agents of pests of trees in urban areas, including residential areas, streets, parks, and urban forests, there are many studies that have documented the effect of ants as biological control of pests of trees in forests (COTTI 1963, ADLUNG 1966, LAINE & NIEMELÄ 1980) and tree crops (THURMAN & al. 2019). A study quantifying predation on artificial caterpillars along an urbanization gradient concluded that ants were responsible for only 4.7% of the attacks in forests but that the percentage increased to 11.3% in suburban and 16.4% in urban forest fragments (FERRANTE & al. 2014). This effect can be explained by higher abundance of generalist predators like ants, as urbanization proceeds.

Ant-mediated pest control services are frequently accompanied by disservices, such as increases in hemipteran mutualists, some of which are vectors of plant diseases, and reduction of other natural enemies. In the following section we discuss these predator-prey and mutualistic interactions in the context of urban ecosystems.

Predator-prey and mutualistic interactions in the context of urbanization

Although most of the studies cited above demonstrate the important role of ants in pest control in urban environments, few of them examine trophic interactions in the context of the process of urbanization. Little is known about how urbanization affects the strength of species interactions (SHOCHAT & al. 2006). Since ants are generalist predators, they are better able to exploit urban environments compared with specialist predators. Furthermore, their mutualistic associations with hemipterans allow ants to exploit disturbed habitats. However, both of these ant traits (generalist predators and mutualistic associations with hemipterans) can have detrimental effects on plants by reducing other predators and increasing sap-sucking insects.

The few studies that have examined the effect of urbanization on arthropod predator-prey interactions have found that urban structures, like roads and buildings, are negatively associated with specialist predators but do not seem to affect generalist predators, such as most ants (SORACE & GUSTIN 2009, RAUPP & al. 2010, BURKMAN & GARDINER 2014, ROCHA & FELLOWES 2020). This is congruent with the long-supported idea that habitat loss and fragmentation are more important for monophages and other habitat specialists than for polyphages or generalists, given that specialist communities and populations are more tightly linked to their particular resources (LAWTON 1995, ZABEL & TSCHARNTKE 1998, RYALL & FAHRIG 2006). Generalist predators, like most ants, are better able to adapt to varying habitat conditions and prey availability (CLAVEL & al. 2011). Furthermore, due to the complexity of the urban matrix, urbanization is likely to affect the

efficiency at which specialist predators locate their prey, compared with generalist predators (GODDARD & al. 2010, TURRINI & al. 2016). In one of the few studies that examined trophic-level interactions and urbanization, ROCHA & FELLOWES (2020) demonstrated that specialist predators were positively related to the proportion of green spaces, but this was not the case for generalist predators, most of which were ants. Surprisingly, ants were positively associated with urban infrastructures (roads and buildings), but also with plant species richness. Furthermore, predatory ants had a negative effect on other more specialized predators.

This study also examined mutualistic ant-aphid interactions and found a higher level of ant tending in the more urbanized environments. Like predatory ants, mutualistic ants had a negative effect on other more specialized predators (ROCHA & FELLOWES 2020). Through their association with hemipterans and other herbivores, ants can protect pest species and / or interfere with biological control by other species. For example, in urban and peri-urban farms in Cuba, the tropical fire ant, *Solenopsis geminata*, which has been reported to be a predator of some insect pests (RISCH & CARROLL 1982, WAY & HEONG 2009), and the tawny crazy ant, *Nylanderia fulva*, have been reported to cause occasional phytosanitary problems associated with their tending of hemipteran pests (VÁZQUES & FERNÁNDEZ 2007). In the Galapagos Islands, an otherwise successful classical biological control program of a scale insect with an introduced coccinellid beetle was ineffective in urban areas where pest colonies were heavily tended by non-native ant species (*Camponotus conspicuus*, *Solenopsis geminata*, and *Monomorium floricola*) (HODDLE & al. 2013). In Yaoundé, Cameroon, maize plants planted next to houses were reported to have a higher incidence of the corn delphacid, *Peregrinus maidis*, a vector of a viral disease, as compared with maize in vacant lots, farther away from houses and, those plants, in turn, had higher incidence of the pest than maize in rural fields. The difference was attributed to the abundance of ants tending the delphacids in the urban sites. The areas next to the houses were rarely ploughed and had higher densities of ant colonies, while maize plots in vacant lots and fields outside the city were ploughed (DEJEAN & al. 1996). Indeed, this could be a major factor shaping species composition in both urban and agricultural environments. Yet, at least one study failed to document shifts in ant interference with biological control with urbanization. KORÁNYI & al. (2021) examined the impacts of urbanization in Budapest, Hungary, on aphids, mutualist ant species (*Prenolepis nitens*, *Lasius niger*, *Lasius emarginatus*), and predatory arthropod abundance and interactions on field maple (*Acer campestre*). They found that impervious surface, their metric of urbanization, was positively correlated with increases in aphid abundance and decreases in ant abundance, but contrary to their expectations, changes in ant abundance did not alter interactions between aphids and other predatory arthropods. As a result, they conclude that urbanization did not alter the degree

to which ants interfere with biological control of this tree pest.

Ecosystem services by ants in the city: a synthesis

Although the literature on ecosystem services and functions provided by ants is extensive (DEL TORO & al. 2012), the study of ant-mediated ecosystem services in urban environments is limited. We summarize the available literature in Table 1. After an extensive literature review, we found that the ecosystem services that ants provide in the context of urban environments are seed dispersal, soil enhancement, removal of human food waste, and biological pest control (Fig. 3). We note that there appear to be more published studies on the impacts of urbanization on ant-provided ecosystem services in the Americas (Tab. 1), with many fewer studies from other global regions, pointing out an important shortfall in our knowledge. In all of these cases, the ecosystem services that ants provide are highly dependent on the ant species composition. Urbanization is a type of disturbance that tends to favor generalist ants which can have positive or negative effects on the provisioning of ecosystem services.

Specialized seed dispersal by ants, or myrmecochory, occurs in myrmecochorous plant species that have elaiosomes that attract ants. Although myrmecochory occurs in many habitats and many plant species throughout the world, it is best known from some herbaceous plants that occur in temperate forests (LENGYEL & al. 2010). Therefore, it is not surprising that the study of myrmecochory in urban environments tends to be biased toward urban and exurban forests in temperate regions. The few studies that have been conducted on myrmecochory in urban landscapes suggest that seed dispersal by ants is highly influenced by ant species composition with urbanization sometimes enhancing (THOMPSON & MCLACHLAN 2007), and sometimes disrupting seed dispersal (WARREN & al. 2015), depending on the ant species present. Another important factor to consider is the size of the forest patch. Urban forests are usually small and therefore strongly influenced by edge effect that tends to favor aggressive, non-native species, typical of disturbed environments. Invasive species can disrupt myrmecochory by displacing

the ant species involved in tight mutualistic interactions with plants (ZETTLER & al. 2001, CARNEY & al. 2003), resulting in a negative impact on myrmecochorous plant species. The dearth of studies about myrmecochory in urban landscapes provides ample opportunity to enhance our knowledge of this important ecosystem service in cities, and especially in city forests. From the effect of forest size on the density and diversity of myrmecochorous plants, to the impact of ant species behaving like invasive species on distance and direction of seed dispersal, these studies could greatly enhance our understanding of the role played by ants in maintaining biodiversity of herbaceous plants in urban forests. Importantly, more studies need to be conducted in other regions, and especially in the tropics where plant biodiversity is higher.

The role of ants in soil turnover, aeration, water infiltration, and nutrient addition has been well established. But like myrmecochory, very few studies have examined these soil enhancement processes in the context of urban landscapes. More importantly, the few studies available have not measured the ecosystem service directly, but rather implied changes to soil-based ecosystem services based on the changes in species composition caused by urbanization. The most urgent need for research in this area is establishing a direct connection between ant species favored by urbanization and soil processes, like aeration, infiltration, and nutrient addition, and how this ant-mediated ecosystem service is manifested in different urban habitats like, among others, urban forests, parks, urban gardens, vacant lots, city streets, and sidewalks. As suggested earlier, a focus on *Tetramorium* spp., pavement ants, could yield interesting information given the high density of this ant in highly urbanized environments and their habit of nesting underneath sidewalks.

There has been a recent interest in the study of ants as scavengers of human food waste in cities. Several studies have quantified the amount of human food waste removed by ants in cities and it turns out to be substantial (PENICK & al. 2015, HOSAKA & al. 2019). The removal of human food waste by ants is beneficial because it can reduce the resources available to more noxious urban pests like rats and cockroaches. Like for other ant-mediated ecosystem services, ant species composition turns out to be a key

Tab. 1: Summary of ant-mediated ecosystem functions and services.

Ecosystem Function / Service (Disservice)	Example	Ant Species Most Responsible	Habitat, City, Country	Direct or indirect Measurement; Increase or Decrease Function in urban sites	Reference
Seed dispersal	Removing seeds of the myrmecochorous plant <i>Viola pubescens</i>	<i>Formica glacialis</i> , <i>Lasius pallitarsis</i> , <i>Myrmica detritinodis</i>	Urban forests, Winnipeg, Manitoba, Canada	Indirect; Increased in urban forests	THOMPSON & MCLACHLAN (2007)
	Removing seeds of several myrmecochorous plant species	<i>Aphaenogaster</i> spp.	Exurban forests, Macon and Madison counties, NC, USA	Indirect; Decreased near exurban forest edges	WARREN & al. (2015)

Ecosystem Function / Service (Disservice)	Example	Ant Species Most Responsible	Habitat, City, Country	Direct or indirect Measurement; Increase or Decrease Function in urban sites	Reference
	Removing seeds of native and non-native plants	<i>Linepithema humile</i>	Urban park near Melbourne, Australia	Direct; more variable dispersal rates and dispersal distance in invaded sites	ROWLES & O'DOWD (2009)
Soil aeration / water infiltration (aerators)	Building subterranean tunnels that facilitate soil aeration and water infiltration	<i>Formica cf. sibilla</i> , <i>F. sibilla</i> , <i>F. lasioides</i>	Urbanization gradient; Lake Tahoe Basin, NE and CA, USA	Indirect; Decreased	SANFORD & al. (2009)
	Building many nest chambers that facilitate soil turn over, aeration and infiltration	<i>Acromyrmex subterraneus molestans</i>	Undescribed urban areas, Juiz de Fora, Minas Gerais, Brazil	Indirect; Increased (nest in urban areas have significantly more chambers than nests in rural areas)	SANTOS LOPES & al. (2011)
	Building nests and foraging tunnels that facilitate soil aeration and water infiltration	<i>Tetramorium immigrans</i> (formerly known as <i>T. caespitum</i>)	Urban sidewalks, Raleigh, NC, USA	Indirect; Increased (ants nesting under pavement, sidewalks and bricks)	NUHN & WRIGHT (1979)
Decomposition (decomposers)	Building tunnel networks in woody debris facilitating decomposition and nutrient release	<i>Camponotus modoc</i> , <i>F. accreta</i>	Urbanization gradient, Lake Tahoe Basin, NE and CA, USA	Indirect; Decreased	SANFORD & al. (2009)
Nutrient addition (compilers)	Built thatch mounds that increase nutrient availability and adds heterogeneity to soil	<i>F. obscuripes</i> , <i>F. ravidata</i>	Urbanization gradient, Lake Tahoe Basin, NE and CA, USA	Indirect; Increased	SANFORD & al. (2009)
Food scavenging	Retrieving food waste from urban areas	<i>Tetramorium sp. E</i> (formerly known as <i>T. caespitum</i>)	Several urban habitats, New York City, NY, USA	Direct; Measurements only within the city	PENICK & al. (2015)
	Retrieving food waste from median in the city	<i>Tetramorium sp. E</i> (formerly known as <i>T. caespitum</i>)	Several urban habitats, New York City, NY, USA	Direct; Measurements only within the city – removal higher in median in the city than in parks	YOUNGSTEADT & al. (2015)
	Retrieving food waste from urban areas (urban and suburban woodlands, lawns and pavement)	<i>Tetramorium tsushimae</i>	Tokyo, Japan	Direct; removal higher in lawns than pavement and woodlands	HOSAKA & al. (2019)
	Retrieving dead arthropods	<i>Anoplolepis gracilipes</i> , <i>Monomorium pharaonis</i> , <i>Paratrichina longicornis</i> , <i>Pheidole megacephala</i> , <i>P. parva</i> , <i>Tapinoma melanocephalum</i>	Singapore (within the University of Singapore)	Direct; Decreased	TAN & CORLETT (2012)
	Removing dead cockroaches from latrines	<i>Pheidole rugaticipes</i> , <i>Pheidole decarinata</i> , <i>Pheidole sp.</i> , <i>Camponotus maculatus</i> , <i>Paratrechina longicornis</i> , <i>Crematogaster sp.</i> , <i>Brachyponera sennaarensis</i>	Nasarawa State, Nigeria	Direct: higher diversity of scavenger ants in urban areas	ASHIGAR & AB MAJID (2020)

Ecosystem Function / Service (Disservice)	Example	Ant Species Most Responsible	Habitat, City, Country	Direct or indirect Measurement; Increase or Decrease Function in urban sites	Reference
Pest control	Predation on house fly eggs, larvae and nearly emerging adults	<i>Solenopsis geminata</i>	Urban areas, San Juan, Puerto Rico	Direct; Measurements only within the city	PIMENTEL (1955)
	Predation attempts on artificial caterpillars	No specific ant species identified	A variety of forests, urban and suburban habitats, Sorø, Denmark	Indirect; Increased	FERRANTE & al. (2014)
	Underground predation on sentinel prey	No specific ant species identified	A variety of urban habitats, Akron and Cleveland, OH, USA	Direct; Measurements only within the cities – predation rate higher in vacant lots than urban gardens	YADAV & al. (2012)
	Predation on sentinel eggs (<i>Helicoverpa zea</i>) and pupae (<i>Sarcophaga bullata</i> and <i>Musca domestica</i>)	No specific ant species identified	Vacant lots and urban gardens, Akron and Cleveland, OH, USA	Direct; Higher removal of <i>Musca domestica</i> pupae in urban gardens as compared to vacant lots in late summer	GARDINER & al. (2013)
	Predation on sentinel eggs of the corn ear worm, <i>Helicoverpa zea</i>	<i>Linepithema humile</i> (most likely)	Urban gardens in three counties in California's central coast, USA	Direct; Smaller gardens experience higher predation services than larger gardens	PHILPOTT & BICHIER (2017)
	Predation on cabbage looper (<i>Trichoplusia ni</i>) larvae and egg clusters	<i>Formica obscuripes</i> , <i>F. subsericea</i> , <i>Tetramorium immigrans</i> (formerly known as <i>T. caespitum</i>)	Urban gardens, Ann Arbor, MI, USA	Direct observations of predations on these sentinel prey	EDWARDS (2016)
	Predation on the sweet potato weevil, <i>Cylas formicarius</i> , and the banana weevil, <i>Cosmopolitas sordidus</i>	<i>Pheidole megacephala</i>	Urban gardens, many cities within Habana Province, Cuba	Direct; Document actual practices among urban farmers	VÁZQUEZ-MORENO & FERNÁNDEZ-CONSUEGRA (2007)
Interference with Biological Control	Ant interference with biological control of a hemipteran pest by other species	<i>Camponotus conspicuus zonatus</i> , <i>Solenopsis geminata</i> , <i>Monomorium floricola</i>	Santa Cruz, Galapagos, Ecuador	Direct; Increased ant tending in urban areas	HODDLE & al. (2013)
	Ant interference with biological control of a hemipteran pest by other species	<i>Solenopsis geminate</i> , <i>Nylanderia fulva</i>	Urban gardens, many cities within Habana Province, Cuba	Indirect; Observations of ant tending in urban areas	VÁZQUEZ-MORENO & FERNÁNDEZ-CONSUEGRA (2007)
	Ants tending hemipterans that are disease vectors of maize	<i>Camponotus acvapimensis</i> , <i>Crematogaster</i> sp., <i>Pheidole megacephala</i>	Yaoundé, Cameroon	Direct; Increased	DEJEAN & al. (2000)
	Invasive ant tending invasive pest species in citrus, <i>Diaphorina citri</i>	<i>Linepithema humile</i>	Several cities in southern California, USA	Direct; <i>D. citri</i> nymphs decreased with higher numbers of other honeydew producers	TENA & al. (2013)
	Ant interference with biological control on field maple (<i>Acer campestre</i>)	<i>Prenolepis nitens</i> , <i>Lasius niger</i> , <i>Lasius emarginatus</i>	Budapest, Hungary	Direct; no effect of urbanization on ant-predator interactions	KORÁNYI & al. (2021)

factor in removal rates. Generalist species with big colonies and high recruitment rates are more efficient removing human food waste than specialized species with small colonies. These are the species that tend to dominate highly disturbed urban habitats such as street medians and are the species that have been documented to have the higher removal rates in cities like New York and Tokyo. Future studies should expand the geographic range of these studies to see if temperature, by increasing size and activity of ant colonies, also increases removal of food waste. As mentioned before, another area that should be explored in future research is how the availability of other resources, like mutualistic hemipterans, affects removal of human food waste in different urban habitats and during different seasons.

The last ecosystem service examined in this review is that of biological pest control. As generalist predators, ants have important impacts on herbivores and are important biological control agents in agricultural areas (ANJOS & al. 2022). However, ants also can reduce populations of pests in non-agricultural contexts, like apiculture, forestry, and even in the public health arena by controlling vectors of diseases. Ants reduce pest damage in urban food gardens and remove sentinel pests in gardens and other urban habitats (VÁZQUES & FERNÁNDEZ 2007, YADAV & al. 2012, GARDINER & al. 2013, FERRANTE & al. 2014, EDWARDS 2016, PHILPOTT & BICHER 2017). But, when evaluating the benefit of ants as pest control of herbivores of plants, it is also important to consider other trophic interactions involving ants that may result in a net negative impact on the plants. Most ants are generalist predators and can prey or compete with other predators, effectively interfering with biological control by generalists and specialist predators or parasitoids (VÁZQUEZ & FERNÁNDEZ 2007, HODDLE & al. 2013, ANJOS & al. 2022). Also, many species of ants tend hemipterans which are themselves pests of plants (TENA & al. 2013) and vectors of plant pathogens (BUCKLEY 1987, DELABIE 2001). However, it is frequently the case that when ants are tending hemipterans on plants, they increase their foraging activity on those plants and can reduce herbivores that cause more damage to the plants than the hemipterans (STYRSKY & EUBANKS 2007).

All these ecosystem services have been examined in the context of public and communal lands, like street medians, city parks and forests, vacant lots, and urban food gardens. However, ants can also provide these ecosystem services in residential areas, inside and outside the living quarters. Unfortunately, there is a strong prejudice against ants in residential areas, and they are frequently considered pests inside buildings (KLOTZ & al. 2003, CAMPOS-FARINHA 2005, SILVERMAN 2005). Indeed, there is a large literature of ants as pests in hospitals and other buildings, with an emphasis on how to control them, usually with pesticides (OLAYA-MASMELA & al. 2005, DE CASTRO & al. 2016). Just recently have the benefits of ants as ecosystem-service providers been recognized. But the long-standing prejudices against ants still prevail. Future research that objectively investigates the positive and negative impact of ants in

residential areas is needed. Some potential future research questions could address, for instance, (1) What is the role of ants as control agents of cockroaches within residential buildings? (2) Are ants controlling pests of backyard gardens or generating more pest problems through their mutualistic association with hemipterans? and (3) Do ants help aerate soil and increase water infiltration, preventing backyard flooding in residential areas?

All the ecosystem services discussed in this review are highly influenced by the species composition of the ant community in urban landscapes and in the different habitat patches within cities. The ant species composition is affected not only by the disturbance created with urbanization but also by the changing climate. In the next section, we discuss the effect of climate change on the ant communities in urban landscapes and how it interacts with the ecosystem services discussed above.

Effect of climate change on ants in cities

Climate change is not only predicted to increase the mean global temperature by 1.7 ° to 4.8 ° C by the end of the century but also to increase extreme climatic events (such as higher maximum temperatures and duration of high temperature events), increase variability in temperature and precipitation (IPCC 2014, PENDERGRASS & al. 2017, BATHIANY & al. 2018), and amplify seasonal cycles (i.e., warming becomes systematically stronger in mid-latitudes during summer) (SANTER & al. 2018). Warmer temperatures will tend to influence ant populations directly through effects on survival, fecundity, generation time, and dispersal. Although individual species responses will depend on their geographic ranges and natural history, it is expected that ant populations in mid to high latitudes will benefit the most from a warmer climate (PELINI & al. 2011, 2012). Since urban environments tend to be warmer than their surroundings (due to the heat island effect; IMHOFF & al. 2010), ants in cities may be indicators of future changes in the ant community associated with climate change (MENKE & al. 2011).

Temperature and water tolerance in urban ants

Applying generalized linear models to a global data set of local ant assemblages, JENKINS and colleagues (2011) found temperature to be the most important single predictor of ant species density, suggesting that climate change could have important consequences for ant species richness and the structure of ant communities. Using predictive models for physiological thermal tolerances in ants based on current and future climates, DIAMOND and colleagues (2012) found that tropical ants will have lower warming tolerances to climate warming than temperate ants. Refining their model with climatic, ecological, and phylogenetic data, they found that ants occupying warmer and more mesic forested habitats at lower elevations, in particular those that live in canopies of tropical rainforests, were the most at risk, globally, from climate warming (DIAMOND & al. 2012).

A handful of studies have examined temperature tolerance in urban ants speculating on ecological and evolutionary impacts. In a study in Raleigh, NC, MENKE and colleagues (2011) tested if the city had a higher proportion of ants from warmer / dryer environments than the surrounding areas. They found that native ant assemblages in open environments within the city have more southwestern (i.e., warmer / drier) distributions than forest assemblages outside the city. The subset of species adapted to warmer / drier environments suggest that urban areas may facilitate the movement and perhaps spread of species adapted to warmer conditions. It is also possible that species with tolerance to climatic extremes may be favored by urban environments. An alternative explanation for the results of MENKE and colleagues (2011) could be that cities favor soil-nesting species rather than cavity nesters (FRIEDRICH & PHILPOTT 2009) or species that nest in rotten wood (VEPSÄLÄINEN & al. 2008). Since species from warmer and drier environments tend to be soil nesters, one may expect a higher proportion of those species in the city as compared with the forested surrounding habitats. Regardless, the findings of MENKE & al. (2011) are supported by a study that directly measured high and low temperature tolerance of urban ants as compared with ants from the surrounding cooler habitats. The study, conducted with the leaf cutter ants, *Atta sexdens*, collected from the city of Sao Paulo and its surroundings, found that ants from the city tolerate heat stress better than ants from their rural surroundings and that this increased temperature tolerance did not come at the expense of tolerance to lower temperatures (ANGILLETTA & al. 2007). A similar finding was reported by WARREN and colleagues (2018) for *Aphaenogaster* spp. in Buffalo, NY. However, DIAMOND and colleagues (2017, 2018) compared thermal tolerance limits for urban and rural acorn ants, *Temnothorax curvispinosus*, from Cleveland, OH, Cincinnati, OH and Knoxville, TN in a common garden experiment finding that ants in urban areas could better withstand higher temperatures but were less able to tolerate cold temperatures. They attributed this temperature tolerance tradeoff to phenotypic plasticity, but also evolutionary changes over just 20 generations of acorn ants because the response to hot and cold temperatures differed based both on source population and rearing temperature.

Ants may also be susceptible to water availability, which may interact with ant physiology to influence thermal tolerance, ant diets, and thus both urban ant communities and the ecosystem services they provide. For instance, in urban areas in California's Central Valley, JOHNSON & STAHLSCHEMIDT (2020) examined the role of water availability, body size, and ant identity as either native or non-native species for thermal tolerance limits. They found that overall, water availability was positively associated with ant body-water content, and that ants, as a community, have a threshold above which water limitation affects their thermal tolerance. Yet, individual ant species responded in quite different ways to short- and long-term water limitation, with some ants highly sensitive to short-

term (8h) water limitation (e.g., *Prenolepis imparis*), others not sensitive (e.g., *Pogonomyrmex californicus*), and still others sensitive to long-term water limits (e.g., *Formica moki*). They also found that the native ants are more sensitive to temperature changes than the non-native ants due to their water limitation. Under changing climates, each of these results could contribute to shifts in ant composition. In a second study, BECKER & MCCLUNEY (2020) examined shifts in arthropod preferences for lipid versus protein diet along an urbanization gradient with or without supplemental water in Toledo, OH. They found that arthropods generally were driven towards lipid diets in more urban sites and that this result was at least, in part, driven by water limitation. In particular, ants (primarily *Camponotus* spp., *Solenopsis molesta*, and *Tetramorium immigrans*) were more commonly occurring on lipid diet stations in sites without supplemental water, and they suggest that such a shift in dryer sites might strongly alter the ecosystem services that ants provide, such as food waste removal.

Interactions between temperature increases and urbanization mediated by biogeography

Interactions between climate change and urbanization may also have impacts on ant behavior and reproduction and seem to be mediated by biogeography. For instance, a study of the black garden ant, *Lasius niger*, which is a common ant in urban areas in northern and temperate Europe, showed lower survival rates of workers at lower overwintering temperatures but no effect of higher or lower overwintering temperatures on queens (HAATANEN & al. 2015). This suggests that urban areas could be acting as a refuge for this species in higher latitudes and could be contributing to its northward expansion (VEPSÄLÄINEN & al. 2008). Warm urban areas and fluctuating snow cover due to climate change could affect the energetics of ants that overwinter beneath the snow (LEATHER & al. 1993). But the ability of founding queens of *L. niger* to tolerate temperature variation present in urban environments, suggests that this species may be one of the winning species in a warmer climate (HAATANEN & al. 2015). GIPPET and colleagues (2017), studying seven ant species in urban areas in Lyon, France, concluded that a species response to urbanization depends on the climatic context along latitudinal and altitudinal gradients, suggesting that a species could be an urban avoider at lower latitudes (hot and dry) and an urban exploiter at higher latitudes (cold and wet). Likewise, in a study of woodland ants along an urbanization and a coastal-to-interior gradient, WARREN and colleagues (2018) suggested that ant responses to urbanization are influenced, or even superseded, by climate change mediated by large bodies of water. In this study, they found physiological, behavioral, and community responses to seasonal coastal-to-interior climate inversions from the Great Lakes, frequently overshadowing the urbanization effects. Interestingly, in *Aphaenogaster* ants, physiological cold tolerance appears to be affected by the closeness to the lake, with lower

tolerance near the lake, while heat tolerance was better predicted by urbanization, with higher tolerance in the cities. They also reported a decline in the range of temperature tolerance with distance from both cities and coastal areas.

One study has documented strong phenotypic impacts of urban heat-island effects on ant reproduction. CHICK and colleagues (2019) studied impacts of heat islands on *Temnothorax curvispinosus* across three cities in the midwestern United States and found that higher urban temperatures advanced peak alate flight dates by one month compared with rural populations, with important implications for breeding and genetic isolation. Urban and rural ant populations may already experience genetic isolation due to fragmentation and dispersal limitation; this study shows that temperature-related effects of urbanization may exacerbate the impacts of other aspects of urbanization.

Do changes in temperature favor invasive behavior and tramp species in cities?

It has been speculated that climate change could facilitate establishment and expansion of invasive species. However, in a recent review, BERTELSMEIER and colleagues (2015) concluded that it is unlikely that global warming will systematically increase ant invasions. What is clear is that several ant species, not necessarily invasive species, will benefit from more suitable, warmer climates and therefore have the potential for further spread (VEPSÄLÄINEN & al. 2008, HAATANEN & al. 2015). Yet, the ability of invasive and tramp species to increase their long-term fitness will depend on phenotypic plasticity and / or appropriate genetic variability resulting in appropriate coping with climate change. Species with narrow phenotypic plasticity will likely experience a decrease in fitness (at least short term), while more plastic species will be able to cope better with climate change (PELINI & al. 2012). However, ants exposed to higher climatic fluctuations, as is the case in most urban environments (IMHOFF & al. 2010), could be selected for higher phenotypic plasticity, enhancing their ability to cope better to a changing climate.

The urban heat-island effect can offer opportunities for exotic ants adapted to warmer climates (BERTELSMEIER & al. 2015). Tramp species common in urban areas have a broad range of temperature tolerance. For example, *Monomorium floricola* and *Tetramorium bicarinatum* tolerate temperatures up to 30 - 50 °C, yet also tolerate very low temperatures (SOLIS & BUENO 2012). In another study, *Solenopsis invicta* had a LT50 (temperature lethal to 50% of individuals) of 43.5 °C after one hour exposure (XU & al. 2009). However, even though opportunistic species may be more tolerant to heat stress or other stressful conditions, they may not outcompete native species adapted to temperature extremes. For instance, WALTERS & MAKAY (2004) found that two native ant species in Australia tolerate higher extreme temperatures than the exotic *Linepithema humile*. Likewise, HOLWAY & al. (2002b), comparing the temperature tolerance of *L. humile* with five native species,

found *L. humile* to be the least tolerant to high temperatures. Naturally, physiological tolerance is not the only response that ants may have to changing climate, with behavioral responses including changing foraging time and building nests deeper into soil (HOLWAY & al. 2002a).

Using a landscape genetics approach, a study examining the effect of climate-urbanization interaction on the distribution of *Tetramorium immigrans* in southeastern France found that in the north of its range, this species can persist under harsher climates by colonizing highly urbanized areas (CORDONIER & al. 2020). The authors of this study suggest that *T. immigrans* might not be a native species in the northern range of the study area and propose that it got there through human introduction subsequent to the expansion of urban areas and behaves as an invasive species in northern cities (see also BOROWIEC & SALATA 2018).

Do changes in precipitation favor invasive behavior and tramp species in cities?

Climate change models also predict changes in precipitation, with higher levels of precipitation in some regions and lower levels in others. These changes will have important consequences for ant communities in urban areas and adjacent natural habitats. In California, *Linepithema humile* invades riparian forest and coastal sage scrub fragments of natural habitat from the urban edge but penetrates drier coastal sage scrub to a distance of only 200 to 250 m (SUAREZ & al. 1998). It has been hypothesized that increased soil moisture near edges due to urban runoff allows expansion into dryer natural habitat (SUAREZ & al. 1998, MENKE & al. 2007). However, BOLGER (2007) failed to find support for this hypothesis since there were no differences in downslope edges versus upslope edges, which would be expected if urban runoff was the main mechanism of facilitated spread. Instead, he found that soil type was most important, with soils that retain more moisture supporting Argentine ant invasion more than well-drained, coarse soils. There is no question that humid conditions facilitate Argentine ant invasion in drier environments. Argentine ants are less resistant to desiccation than native ants in arid regions of California (HOLWAY & al. 2002a, b) and Australia (WALTERS & MACKAY 2004). El Niño events, which increase total rainfall in the San Diego area, have been increasing in frequency since the 1970's (TRENBERTH & HOAR 1997), supporting the climate change models that also predict increased El Niño frequency (TIMMERMAN & al. 1999). Taking this into account, recent niche modeling analyses suggest that predicted climate change will lead to increases in the introduced ranges of Argentine ants worldwide (ROURA-PASCUAL & al. 2004, 2009). However, in regions where drier conditions are predicted, lower soil moisture may prevent invasions or further expansions of the Argentine ant. This suggests that invasive ants may not systematically benefit from climate change as has been assumed (BROOK & al. 2008, HELLMANN & al. 2008). Indeed, modeling suitable global areas for 15 of the worst ant invasive species, BERTELS-

MEIER and colleagues (2015) found that only five of those species were predicted to increase with climate change. Given the importance of multiple factors such as soil type, soil moisture, and ambient temperatures for particular ant species, examining specific influences of soil and substrate temperatures (in addition to ambient temperatures) could reveal important information on success of certain ant species in urban environments, depending on their nesting habits.

Climate change can affect ant species interactions

While the impact of a changed climate on the potential for changing ant communities is a common theme in the literature (JENKINS & al. 2011, MENKE & al. 2014, DIAMOND & al. 2016), the indirect consequences on how such changes might affect the interactions among ants as well as the interactions of ants with other elements of the local biological community have not been explored in depth. It is well known, for example, that changes in microclimatic conditions can alter competitive interactions among ants (PERFECTO & VANDERMEER 1996), suggesting that climate-mediated changes in ant interactions could also facilitate some species. For example, Argentine ants remain active throughout summer afternoons in Northern California while competing indigenous ants, less tolerant of high temperatures, become inactive (HUMAN & GORDON 1997). Such a pattern could provide a competitive advantage to the Argentine ant under global warming scenarios. Furthermore, temperature changes in urban environments that affect native species could create appropriate conditions for establishment of invasive species (the priority effect) (VEPSÄLÄINEN & PISARSKI 1982, PHILPOTT 2010), or nonlinear complications related to the so-called insinuator / dominator tradeoff in competitive interactions (YITBAREK & al. 2017). Effects of competition in the urban environment are known for *Linepithema humile* (TOUYAMA & al. 2003, MENKE & HOLWAY 2006), and the potential for climate change to alter these interactions are certainly palpable. Climate-driven changes may also affect species-specific interactions in ant-plant mutualisms (WARREN & CHICK 2013) and ant-hemipteran mutualism (ZHOU & al. 2017).

Conclusions and future directions

There is general consensus that ants are of immense importance in their effects on terrestrial ecosystems generally, and specifically on human-built ecosystems such as agroecosystems and managed forest ecosystems (HÖLLDÖBLER & WILSON 1990, FOLGARAIT 1998, DE BRUYN 1999, PHILPOTT & ARMBRECHT 2006, VANDERMEER & PERFECTO 2007, PHILPOTT & al. 2009). Yet, the ubiquity of ants in most urban environments has only recently attracted the attention of myrmecologists and ecologists more generally (STRINGER & al. 2009). Much of that interest has classically been focused on ants as those pesky visitors to family picnics and sugar bowls in the kitchen, with the implied need to exert the exterminator's wand (SILVERMAN 2005).

More recent literature acknowledges that there is a host of interesting questions to be asked about the assemblage of ant communities within this other highly artificial environment called "the city."

Within this newer literature, there is a trend towards framing the ant question within the popular framework of ecosystem services, which is another way of saying that ants are not only pests in the urban environment, but also engage in particular activities that might be viewed by humans as beneficial in one way or another. Here, we have reviewed a selection of the literature that focuses on this aspect of urban ants.

One important area revealed by this review is that landscape features are important determinants of ant diversity and community composition, yet studies of landscape determinants of ant-provided ecosystem services are rarer. For example, proximity to natural habitat and forest reserves can facilitate maintenance of ant diversity in urban parks (PACHECO & VASCONCELOS 2007). Likewise, distance from an urban core promotes arboreal ant diversity (SANTIAGO & al. 2018). The shape and size of urban forest fragments can strongly influence ant communities therein, likely through edge effects that change environmental conditions and favor generalist and non-native species (ACHURY & al. 2021, MELO & al. 2021). Moreover, factors such as landscape connectivity achieved by continuous plant cover in older residential neighborhoods can act as a barrier to ant invasion (PLOWES & al. 2007). Despite these results, there is still a relative lack of studies on the landscape characteristics that may influence ants in urban environments, and especially the landscape mediation of ant-provided ecosystem services.

A second important conclusion to derive from the few studies that are available at this time, is that the potential for ants to provide ecosystem services in urban areas depends on how the ant community is affected by urbanization and the resulting species composition. In some cases, the remaining species are highly effective, like in the case of the pavement ants scavenging on food waste in New York City (YOUNGSTEADT & al. 2015) and the ants dispersing the myrmecochorous violets in urban parks in Manitoba (THOMPSON & MCLACHLAN 2007). However, in other cases, the most efficient species decline or are replaced by less efficient species as urbanization proceeds, as in the case of the replacement of aerators and decomposer species by more generalist ant species in the urban forests in the Lake Tahoe basin (SANFORD & al. 2009).

There can be no doubt that some of the classic ecosystem services cited by ecologists are performed to one degree or another by various ant species. Whether speaking of seed dispersal, soil modifications, scavenging, or biological control, it is evident that such services frequently are at least partly provided for by ants. The issue of invasiveness is a frequent intellectual hitchhiker in these narratives, effectively asking to what extent does invasive species X interfere with the normal ecosystem services provided by the "native" ants already there, perhaps an unusual question in the end, since being "native" to a city is

perhaps not a well-formed concept to start with. Furthermore, there are a number of cases where the most efficient ecosystem-service provider is a non-native species, like the scavenging pavement ant in Manhattan (PENICK & al. 2015) or the pest-removing Argentine ant in California (PHILPOTT & BICHER 2017).

The other element of urban ant biology that has come under considerable scrutiny recently is the expected effects of climate change on the urban ant community. Here, we have much speculation, based on extrapolations from underlying concepts, mainly based on physiological assumptions. As temperatures increase and as rainfall becomes less regular, the basic physiological processes that constrain ectotherms in general, and ants specifically, can be easily tied to what we might expect from climate change. The fact that urban environments are warmer, and in some cases wetter, than their surrounding rural or natural environments makes cities a window into the future of ant communities under climate change. What we see through that window is that the ants that persist in urban environments are those with broader temperature ranges and higher heat tolerance, whether it is through an increase in the minimum temperature or the maximum temperature that ants can tolerate. But we have to be cautious in making this conclusion since there are strong urbanization-climate interactions. We add to that concern the fact that ants interact with other arthropods (and other taxa), and especially with other ants, to form communities and ecosystems, and it is sometimes the case that the perhaps subtle ensuing interactions are the elements that provide ecological structure. It is precisely this intersection of urbanization, climate change, and ant ecological interactions that present us with the greatest opportunity for future studies. In particular, the interaction between climate change, urbanization, and invasive behavior in ant species deserves more attention since climate change and urbanization may favor invasive behavior, which could in turn affect ecosystem services provided by ants, in positive and negative ways. Future studies could also focus on functional redundancy of different ant species to see if shifts in community composition with urbanization or climate change or both are more important determinants of ecosystem services than ant diversity alone. Another example is the possibility of having climate-mediated winners and losers in myrmecochorous plants due to asynchronies that emerge from different responses to climate change of ants and their plant partners (WARREN & CHICK 2013). How would these asynchronies play out in urban forests where temperatures are likely to be higher and where urbanization tends to favor more generalist species, and what would the impact be on myrmecochory? More generally, future research could be guided by the question of how the results of climate change will affect the elements that provide ecological structure in ant communities, and what changes result from this for ant-mediated ecosystem services. This question remains understudied and is undoubtedly an important theme for future study.

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